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Research Article

Reducing Effort While Improving Inference: Estimating Dall's Sheep Abundance and Composition in Small Areas

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ABSTRACT Recent work has demonstrated that aerial distance sampling surveys are more efficient and effective than unadjusted minimum count surveys for estimating Dall's sheep (*Ovis dalli*) abundance, although large sample size requirements (e.g., 150–200 detections) may discourage implementation of these methods in small (<2,500 km^2) or low density areas. However, a Bayesian analytical approach using informed priors and borrowing detection information across surveys can increase precision and decrease required sample sizes. Using these methods, we conducted distance sampling surveys across a majority of the Dall's sheep habitat within National Park Service units in Alaska during 2010–2011. We compared 4 analytical scenarios using increasing amounts of detection information to demonstrate the increases in efficiency that can be gained over time through the use of this approach. Based on our analysis using all available survey information in the estimation of the detection function, we estimated that 2,252 (1,871–2,765), 2,809 (2,361–3,379), 1,669 (1,339–2,120), and 12,428 (10,780–14,470) sheep occurred in Denali National Park and Preserve (DENA), the Western Arctic National Parklands (WEAR), the Itkillik preserve subarea of Gates of the Arctic National Park and Preserve, and Wrangell-St. Elias National Park and Preserve (WRST), respectively. These estimates were achieved with relatively small numbers of group detections in DENA ($n = 57$), the Itkillik preserve area ($n = 48$), and WEAR ($n = 100$), suggesting that sample size requirements for Dall's sheep distance sampling surveys can be reduced by an additional 50–75% over previously recommended levels when adequate prior information is available. In addition, we describe a formal approach for estimating the size of individual composition classes (i.e., lambs, ewe-like sheep, <full-curl rams, ≥full-curl rams) and sex and age ratios, corrected for incomplete detection. We implemented the composition analysis within the distance sampling analytical framework as part of the abundance estimation process. This approach to the estimation of population composition could replace commonly used indices and provides more detailed and rigorous estimates that are directly comparable among survey areas and years. We found that ratios of ≥full curl rams:100 ewe-like sheep in WEAR and Itkillik preserve subarea populations were less than in the DENA population, whereas lamb:ewe-like ratios were similar across all 4 survey areas, suggesting relatively consistent productivity. We recommend that aerial distance sampling survey methods using prior information, combined with direct estimation of population composition, be used to increase the effectiveness of Dall's sheep population monitoring and management throughout their range.

KEY WORDS abundance, Alaska, composition, Dall's sheep, detection probability, distance sampling, informed prior, *Ovis dalli*.

Dall's sheep are popular as a game species throughout their range in Alaska and hunter demand has steadily increased through time (Alaska Department of Fish and Game [ADFG] 2008). The ADFG manages most hunts throughout the state (ADFG 2008), but as much as 40% of Alaska's sheep population may reside on United States National Park Service lands (Heimer 1980) where management plans do not prioritize high harvest. Because of the importance of this species for both consumptive and non-consumptive uses, sheep have been selected for long-term monitoring as part of the National Park Service Inventory and Monitoring program in Alaska, requiring precise, cost-effective, and logistically feasible methods for estimating population size and composition at multiple spatial scales (MacCluskie et al. 2005, Lawler et al. 2009). Historically, unadjusted minimum count index surveys have been the primary means used to assess sheep populations, and observed sex and age

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ratios based on these data are then used to assess productivity and inform harvest management (Singer 1984*b*, Udevitz et al. 2006, ADFG 2008, Arthur and Prugh 2010). However, these methods do not include estimates of precision or corrections for imperfect detection and may be less appropriate and cost-effective than other survey methods (c.f., Whitten 1997, Udevitz et al. 2006, Schmidt et al. 2012) for long-term monitoring of different sheep populations. These limitations could lead to inappropriate and inefficient management decisions over large areas, perhaps resulting in long-term population-level declines.

Distance sampling surveys (Buckland et al. 2001, 2004) have recently been shown to produce economical and theoretically sound estimates of Dall's sheep abundance over large areas (Schmidt et al. 2012), although one of the main criticisms has been the large recommended sample sizes (i.e., 150–200 group detections) required for precise estimates (approx. 15% CVs) of abundance. This stipulation can make the distance sampling approach unappealing for smaller management areas (e.g., $<2{,}500\ km^2$) or in areas where densities, and thus detection rates, are expected to be low. Buckland et al. (2001) recommended a minimum of 60–80 detections for basic distance sampling applications; however, samples of this size can produce imprecise estimates that are of limited utility for management. Alternatively, a hierarchical Bayesian approach to analyzing distance sampling data provides the opportunity to build upon existing knowledge over time through the use of informed priors (Gelman et al. 2004, King et al. 2010, Link and Barker 2010) and the borrowing of information across surveys. With several hundred detections from Schmidt et al. (2012), much information about the detection process for Dall's sheep distance sampling surveys is currently available. Rather than assuming no knowledge of the detection process, this information could be used to construct informed priors for new surveys. Additionally, if we assume that the basic form of the detection function is similar between surveys, information about the detection process could also be borrowed across multiple surveys. This would further reduce sample size requirements for individual areas while producing estimates with increased precision. The use of Bayesian hierarchical modeling in this way could thus increase the applicability of the distance sampling approach to additional areas, including smaller units of particular management interest.

In addition to abundance information, managers regularly use estimates of population composition to monitor and manage ungulate populations (e.g., White et al. 1996, 2001; Harris et al. 2008; DeCesare et al. 2012). During most fixed-wing surveys of Dall's sheep, groups are classified as lambs, ewe-like sheep (includes ewes, yearlings, and young rams), $<$full-curl rams ($>$¼ curl and $<$full curl), and $\geq$full-curl rams (includes rams with both horns broken), and simple ratios of lambs:100 ewe-like and rams:100 ewe-like are generated from the raw data (ADFG 2008). However, these indices will be biased if detection probability differs among sex and age classes (Skalski et al. 2005), generally requiring Horvitz–Thompson type estimators incorporating group detection probabilities (e.g., Horvitz and Thompson 1952, Cochran 1977) for proper inference (Skalski et al. 2005). Group size is known to influence detection probability in Dall's sheep (Strickland et al. 1992, Udevitz et al. 2006, Schmidt et al. 2012), and some composition classes such as $\geq$full-curl rams and ewes with lambs may occur in smaller groups on average. Even if detection probabilities were similar across groups, ratios are difficult to interpret because the value used as the denominator is generally the observed number of ewe-like sheep (Harris et al. 2008). Use of this sort of estimator requires the assumption that the proportion of ewe-like sheep in the population does not change over time, as a variety of changes in population structure can lead to the same observed trends in ratios (Caughley 1974, McCullough 1994). Schmidt et al. (2012) proposed a partial solution using the observed proportion of lambs in each group detected during a distance sampling survey to generate estimates of the number of lambs and adults in the population; however, a formal method for estimating the abundance and ratios of multiple sex and age classes in the population, corrected for incomplete detection, was not developed. Simultaneous estimates of abundance and composition, including the estimation of the size of individual composition classes, would produce detection-corrected ratios unaffected by changes in the ewe-like component. This may allow managers to adjust hunting seasons and bag limits based on age cohorts, rather than relying solely on a fixed harvest rate or regime. Combining these data sources in an adaptive management framework may allow more opportunities for harvest over the long term, while reducing the possibility of overharvest in years with poor recruitment (e.g., Hunter and Runge 2004). These benefits could apply to population surveys for any species where composition and abundance data can be collected simultaneously.

During 2010–2011, we conducted aerial distance sampling surveys over a majority of the Dall's sheep habitat in 6 National Park Service units in Alaska, including Denali National Park and Preserve (DENA); Noatak National Preserve, Kobuk Valley National Park, and Cape Krusenstern National Monument (collectively managed as the Western Arctic National Parklands [WEAR]); the Itkillik preserve subarea in northeastern Gates of the Arctic National Park and Preserve (GAAR); and Wrangell-St. Elias National Park and Preserve (WRST). During these surveys, we collected both abundance and composition data for the observed groups, allowing us to jointly estimate abundance and population composition for each area. The number of detections in DENA, WEAR, and the Itkillik preserve subarea were expected to be <150 groups per survey, providing an opportunity to investigate how information from other past and concurrent surveys could be used to produce abundance and composition estimates in smaller or lower density areas. Our primary objectives were to 1) increase the applicability of the hierarchical approach described in Schmidt et al. (2012) to small and/or low density areas where sample sizes were likely to be small, 2) develop methods to directly estimate the abundance of individual composition classes and corresponding sex and age ratios corrected for incomplete detection, and 3) provide current estimates of total population size and composition for each park unit and subarea to help inform future management decisions.

STUDY AREA

Our study area encompassed most of the Dall's sheep habitat in DENA north of the Alaska Range (4,083 km^2), WRST (27,138 km^2), WEAR (15,222 km^2), and the Itkillik preserve subarea in GAAR (2,542 km^2; Fig. 1). Glaciers and ice-fields spanning the Alaska Range limit Dall's sheep habitat in DENA, and divide the main population of sheep on the north side of the range (62°48′–63°50′N and 148°50′–152°7′W) from those populations occupying the mountains to the southwest of the park and preserve. The WRST covers the eastern Chugach Range, western St. Elias Mountains, Wrangell Mountains, and the eastern end of the Alaska Range including the Nutzotin and eastern Mentasta Mountains. Our survey area in WRST (60°37′–62°48′N and 141°0′–144°55′W) covered that surveyed by Strickland et al. (1992, 1993) and ranged from 600 m to 3,350 m in elevation, although most areas above 2,700 m were dominated by ice fields. The WEAR survey area included mountainous portions of the Noatak National Preserve, Kobuk Valley National Park, and Cape Krusenstern National Monument. This area is characterized by rolling hills interspersed with rocky outcrops below 1,365 m in the Igichuk Hills and Baird Mountains south of the Noatak River and the higher (<1,530 m), more rugged De Long Mountains north of the Noatak River (WEAR N; 67°8′–68°42′N and 156°47′–163°40′W). The Itkillik preserve subarea (67°55′–68°30′N and 149°20′–151°35′W) spanned the Continental Divide in northeastern GAAR where rugged, glacier-sculpted peaks reach 2,320 m.

Average annual temperatures varied by elevation, latitude, and proximity to maritime climate regimes, ranging from −2° C at 600 m in southern WRST to −12° C at the higher survey elevations in DENA and WRST (Redmond and Simeral 2006), and ranging from −6° C in the western Baird Mountains to −14° C at the highest elevations in the Itkillik preserve subarea for the Brooks Range survey areas (Davey et al. 2007). The Chugach Mountains in WRST were more glaciated and received greater snowfall than the Wrangell and St. Elias Mountains in the northern portion of the WRST survey area (National Park Service 1986). The predominant vegetation was alpine tundra composed of *Dryas* sp., lichens, mosses, and forbs on well-drained slopes and ridges at higher elevations, shrub birch and willow at lower elevations in WRST and DENA, and wet to moist tussock tundra on gentler slopes in WEAR and the Itkillik preserve subarea.

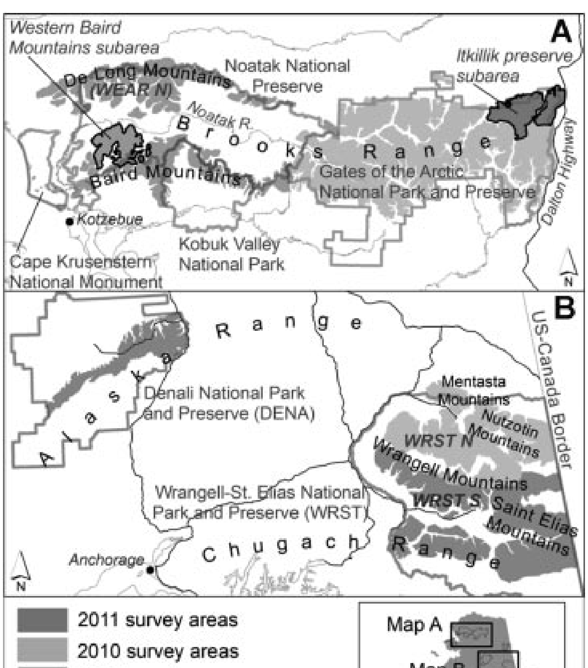

Figure 1. Areas surveyed for Dall's sheep in 2010 and 2011 by the National Park Service (NPS) in Alaska, USA. Estimates of abundance and composition were generated for each park unit as well as smaller subareas of management or monitoring importance. Cape Krusenstern National Monument, Kobuk Valley National Park, and Noatak National Preserve are managed as the NPS Western Arctic National Parklands (WEAR); these park units were surveyed and the data analyzed together.

METHODS

Sampling Design and Field Procedures

We surveyed a portion of WRST including the northern Wrangell, Nutzotin, and Mentasta mountain ranges in 2010 and DENA, WEAR, the Itkillik preserve subarea, and southern WRST in 2011 (Fig. 1). The survey areas included all historically surveyed Dall's sheep habitat in and adjacent to each park unit based on past work (Singer et al. 1983; Singer 1984*a*, *b*; Strickland et al. 1992; Shults 2004). Survey design closely followed that described by Schmidt et al. (2012), although transect spacing and length varied by park unit depending on the size of the survey area and expected sheep densities. In DENA, we considered mountainous areas between 914 m and 1,981 m to be potential habitat. We narrowed this to the north side of the Alaska Range, removed large glaciers and ice fields, and then generated 15-km transects ($n = 84$) centered on the corner points of a 7-km grid with a random start covering the resulting survey area. In WEAR, we included all areas delineated as sheep habitat by Singer et al. (1983), including the Wulik Peaks northwest of WEAR, and added contiguous areas above 350 m in the upper Squirrel River drainage, the Kallarichuk Hills, and west of the Nakolik River to Kanaktok Mountain as well as areas above 300 m from Deadlock Mountain to the Kelly River. We generated a 6-km grid and 15-km transects ($n = 43$) in the historically surveyed western Baird Mountains subarea (Shults 2004) to allocate additional effort and provide greater precision for harvest management in that area, and a 7.5-km grid and 20-km transects in the rest of WEAR ($n = 224$). In WRST, we generated 20-km transects ($n = 303$) on a 9.5-km grid throughout the park in areas delineated as sheep habitat by Strickland et al. (1992, 1993). The survey for the Itkillik preserve subarea followed Schmidt et al. (2012), although we used an 8-km grid with a new random starting point to generate the 20-km transects ($n = 39$). Transects followed contours based on the elevation of the corresponding grid location. Where we could not generate full-length transects because of lack of sufficient terrain, we produced multi-part transects by continuing the route in adjacent areas at the same elevation (see Walsh et al. 2010).

We conducted all surveys during the month of July using tandem fixed-wing aircraft (Piper Supercub, Piper Aircraft, Inc., Vero Beach, FL; Aviat Husky, Aviat Aircraft, Inc., Afton WY; and Bellanca Scout, AviaBellanca Aircraft Corporation, Alexandria, MN). We surveyed each transect at approximately 90 m above ground level and the pilot and observer worked together to search for sheep on the uphill side of the aircraft. Because we could not always follow the transect exactly because of terrain and limitations of the aircraft, we used the computer-generated transect as a guide for the pilot and used the actual on-effort flight line traveled as the final transect for all analysis purposes. This ensured that all detection distances and effective area calculations applied to the actual area surveyed. When we detected a group of sheep, the pilot would leave the transect (i.e., off-effort) to mark the initial location of the group with a Global Positioning System (GPS). After marking the location, the pilot circled the group to determine the number of individuals present. We classified sheep into 1 of 5 sex and age composition classes: lambs, ewe-like, $<$full-curl rams, $\geq$full-curl rams, and unclassified (Schmidt et al. 2012). We also took high resolution photographs of groups when needed to help attribute individuals to the appropriate class. We then used the minimum horizontal distance between the group location and the on-effort flight line as the perpendicular distance for analysis. Further details on survey protocols can be found in Schmidt et al. (2012).

Data Analysis

We left truncated all observations at <22 m to account for the partially observed strip beneath the aircraft (Walsh et al. 2010) and right truncated distances >685 m based on the results of Schmidt et al. (2012). We treated the remaining detection distances as the effective width, w, of the sampled strip of each transect (Becker and Quang 2009). We calculated the total area searched on each transect, a_i, using a horizontal buffer with width $w = 663$ m along the on-effort flight line on the uphill side of the aircraft. Because the transects were nonlinear, portions of the area sampled from different locations along a transect could overlap. To calculate the effective area sampled for each transect, we calculated the area of the resulting buffer polygon (Becker and Quang 2009, Schmidt et al. 2012) using ArcMap10.1 (Environmental Systems Research Institute, Inc., Redlands, CA).

We used Bayesian hierarchical distance sampling models (see Royle et al. 2004, Royle and Dorazio 2008, Johnson et al. 2010, Schmidt et al. 2012) to estimate abundance within each park unit or subarea of interest (Fig. 1) and used multiple covariate distance sampling methods (Buckland et al. 2004, Marques et al. 2007) to improve estimator efficiency. This approach uses data-augmentation (Royle and Dorazio 2008), adding an arbitrarily large number of missing values representing potential unobserved groups to be estimated during the Bayesian updating process. Estimates of abundance and density using this method require the estimation of several interrelated sub-models including probability of group presence on a given transect, detection probability, total group size, and number of individuals in each composition class within a group. The data required for analysis were group detections for each transect, the corresponding total group sizes for the observed groups, the observed number of individuals belonging to each of the 4 composition classes within each observed group, the perpendicular distance between each group and the on-effort transect line, and the elevation of each transect. We then estimated these quantities for all unobserved groups during the Markov chain Monte Carlo (MCMC) updating process.

The observed detections of sheep groups, y_{ij}, are a product of incomplete detection and the probability of presence and can be represented by the equation

$$y_{ij} = \hat{p}_{ij}\hat{\Psi}_i$$

where $\hat{p}_{ij}$ is the estimated detection probability for each group j on each transect i and $\hat{\Psi}_i$ is the probability that each potential group is present on transect i. To estimate the probability of presence for each potential group within each park unit, we needed to construct a sub-model for $\hat{\Psi}_i$. We allowed $\hat{\Psi}_i$ to vary by park unit and assumed a curvilinear relationship between the probability of presence and elevation based on our knowledge that sheep tend to occur less often at both low and high elevations. Therefore, this sub-model can be written as

$$\text{logit}(\Psi_i) = (\gamma_{\text{unit}} + \gamma_1 E_i + \gamma_2 E_i^2 + e_i)$$

where γ_{unit} is the park unit-specific intercept, γ_1 and γ_2 are parameters, E_i is the elevation of transect i, and e_i is a mean 0, normally distributed random effect. In the future, other relevant habitat or transect-specific covariates could be easily included when available, although we did not consider additional covariates here.

Based on the results of Schmidt et al. (2012) and preliminary histograms of our data, we assumed that detection probability was well represented by the hazard-rate function

$$\hat{p}_{ij} = 1 - \exp\left(-\frac{x_{ij}}{\sigma_{ij}}\right)^{-b_{\text{unit}}}$$

where x_{ij} represents the perpendicular distance from transect line i of group j, σ_{ij} is scale parameter, and b_{unit} is the park unit-specific shape parameter. If no previous information about the form of the detection function had been available, model selection techniques could have been used to select an appropriate model. In our case, we expected the basic form of our detection process to be similar among surveys; therefore, small differences could likely be addressed through the use of covariates. We wanted to be able to investigate potential differences in detection probability among park units in case there were some systematic differences among them. We also expected that larger groups would be more easily detected, so we included group size, $\hat{s}_{ij}$, as a covariate in the model for σ_{ij}. This model for σ_{ij} can be written as

$$\sigma_{ij} = \exp(\beta_{\text{unit}} + \beta_1 \hat{s}_{ij})$$

where β_{unit} is the park unit-specific intercept and β_1 is the adjustment for estimated group size.

To include group size as a covariate, we also needed to create a sub-model for $\hat{s}_{ij}$. Our formulation differs from the presentation in Schmidt et al. (2012) in that we represent $\hat{s}_{ij}$ as the sum of the estimated number of individuals within each composition class in each group on each transect, rather than as an overdispersed Poisson model. This can be written as

$$\hat{s}_{ij} = (\hat{N}\text{Lambs}_{ij} + \hat{N}\text{Ewes}_{ij} + \hat{N}\text{Srams}_{ij} + \hat{N}\text{Lrams}_{ij})$$

where the sub-models for each of the 4 composition classes are themselves overdispersed Poisson models representing the number of individuals from each of 4 composition classes within each group. These 4 sub-models can be written as

$$\hat{N}Lambs_{ij} = \exp(l.int_{unit} + e.L_{ij})$$

$$\hat{N}Ewes_{ij} = \exp(e.int_{unit} + e.E_{ij})$$

$$\hat{N}Srams_{ij} = \exp(sr.int_{unit} + e.SR_{ij})$$

$$\hat{N}Lrams_{ij} = \exp(lr.int_{unit} + e.LR_{ij})$$

where $l.int_{unit}$, $e.int_{unit}$, $sr.int_{unit}$, and $lr.int_{unit}$ represent park unit-specific intercepts for the estimated number of lambs, ewe-like, <full-curl rams, and ≥full-curl rams in each group, respectively. The terms $e.L_{ij}$, $e.E_{ij}$, $e.SR_{ij}$, and $e.LR_{ij}$ represent mean 0, normally distributed random effects for each group j on each transect i for lambs, ewe-like, <full-curl rams, and ≥full-curl rams, respectively. These random terms were also park unit-specific. By constraining the number of individuals within each of the 4 categories to sum to $\hat{s}_{ij}$, we could then accurately estimate the composition of each group.

After all of these quantities have been estimated, density, $\hat{D}_i$, for each transect is then simply

$$\hat{D}_i = \frac{n_i}{a_i}$$

where n_i is the number of individuals on a transect. This quantity can be calculated as

$$n_i = \sum_{j=1}^{m} \hat{\Psi}_i \hat{E}(s_{ij})$$

where m is the maximum possible number of groups on a single transect. Estimates of abundance for a given area are then calculated by summing the n_i values corresponding to the area of interest, and dividing the proportion of the total survey area covered by the corresponding a_i values.

To facilitate a comparison of the effect of borrowing information about the detection process, we considered 4 different scenarios when estimating the parameters b and σ: 1) diffuse priors [$\sigma_{\text{unit}} \sim N(0,100)$, $b_{\text{unit}} \sim N(0,100)$] and park unit specific detection parameters [σ_{unit}, b_{unit}], 2) informed priors [$\sigma_{\text{unit}} \sim N(0.5,0.04)$, $b_{\text{unit}} \sim N(2.01,0.14)$] and park unit specific detection parameters [σ_{unit}, b_{unit}], 3) diffuse priors [$\sigma. \sim N(0,100)$, $b. \sim N(0,100)$] and common detection parameters among park units [$\sigma.$, $b.$], and 4) informed priors [$\sigma. \sim N(0.5,0.04)$, $b. \sim N(2.01,0.14)$] and a common detection parameters among park units[$\sigma.$, $b.$]. The prior for β_1 was $\sim N(0.106, 0.004)$ for all scenarios with informed priors. The informed prior distributions for the detection parameters were based on the posteriors obtained from the 2 previously completed surveys of GAAR reported on by Schmidt et al. (2012). The priors for the remaining model parameters were diffuse. These scenarios allowed us to assess model performance and the resulting population estimates relative to the amount of detection information shared among sites and projects. Scenario 1 is analogous to conducting and analyzing each individual survey separately, whereas scenario 4 is similar to analyzing all the data from our current work, as well as the data from Schmidt et al. (2012) simultaneously.

We conducted all model fitting using WinBUGS 1.4 (Spiegelhalter et al. 2004) and ran 2 MCMC chains for 50,000 iterations (see Supporting Information for example WinBUGS code, available online at http://onlinelibrary.wiley.com). After discarding the initial 10,000 iterations as burn-in and thinning by a factor of 8, we retained the remaining 5,000 samples from the posterior distribution for each parameter. We used the Gelman–Rubin diagnostic (Brooks and Gelman 1998) to assess convergence and assumed convergence had been reached when the diagnostic was <1.1 for all parameters. We obtained estimates of abundance using the same methods as Schmidt et al. (2012) by first calculating transect-level density estimates and then multiplying these estimates by the area sampled per transect. The result was an estimate of transect-level abundance. We obtained park unit-specific estimates by summing the corresponding transect-level abundances and dividing this value by the proportion of the area sampled. We estimated the abundance of individual population components using the same approach. We calculated sex and age ratios by dividing the total estimated number of individuals in each composition class in each area by the total estimated number of ewe-like sheep in the area. Performing this calculation as part of the updating process also allowed us to produce appropriate measures of precision around each ratio estimate. We presented all estimates as means and 95% credible intervals (CI) based on the posterior distributions.

RESULTS

Effort, sample sizes, and survey efficiency differed among park units and between 2010 and 2011 depending on the amount of potential sheep habitat, weather, and logistical constraints (Table 1). We surveyed most or all transects in each area (Table 1), except for a portion of southern WRST where we were unable to complete 35 transects because of inclement weather. We generated estimates for uncompleted transects through the MCMC updating process, which allowed us to produce estimates that applied to the entire survey area within each park unit. After truncation, 57, 48, 100, and 242 groups remained for analysis for DENA, the Itkillik preserve subarea, WEAR, and WRST, respectively (Table 1).

As expected, the results for park units with low numbers of detections (i.e., DENA, the Itkillik preserve subarea) were more sensitive to the amount of borrowed information about the detection process (Fig. 2, Table 2). When prior information was not included, estimates for DENA and the Itkillik preserve subarea were strongly influenced by relatively few detections at short distances (Fig. 2A and B), likely resulting in overestimates of abundance. Conversely, park units with larger sample sizes were less influenced by additional information from other surveys resulting in more similar estimates under the different scenarios (Fig. 2, Table 2). As more information was used for estimating the detection function, estimates were less dependent on the specific pattern of detection distances in a particular park unit and precision generally increased for all parks (Table 2). The point estimates for units with larger numbers of detections (i.e., WEAR, WRST) did not change dramatically under the different scenarios (Fig. 2C and D, Table 2), suggesting a common detection process among park units. We selected the scenario using the most detection information (i.e., informed priors with a common detection function among park units) for inference. The fitted detection function represented the overall data from all park units quite well (Fig. 3), and the characteristic shoulder and monotonic decline in the number of detections with distance suggested the basic assumptions of the method were met.

Based on the chosen analytical approach, the resulting estimates of the scale and shape parameters closely agreed with past work. The estimate of the shape parameter of the

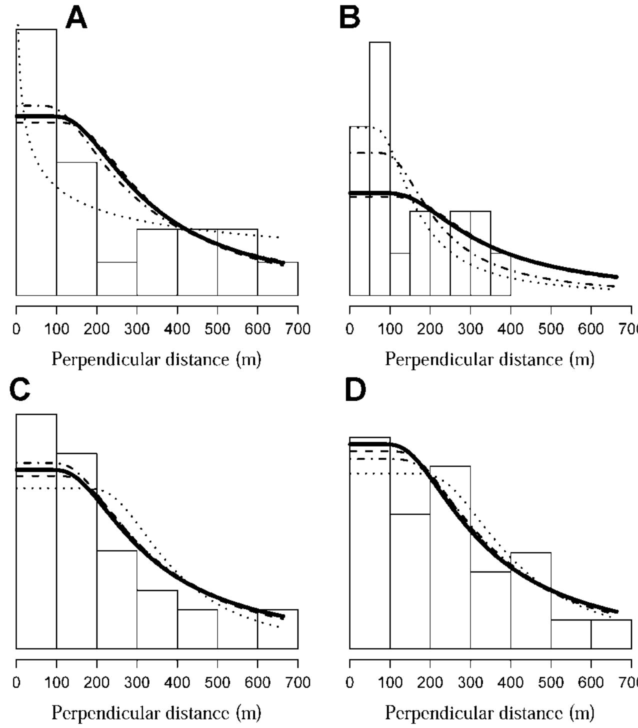

Figure 2. Comparison of fitted detection functions and patterns of observed distances to Dall's sheep groups for each surveyed park unit, 2010–2011. Histograms represent observed relative frequencies of detection distances for all observed Dall's sheep groups in Denali National Park and Preserve (A), the Itkillik preserve subarea of Gates of the Arctic National Park and Preserve (B), Western Arctic National Parklands (C), and Wrangell-St. Elias National Park and Preserve (D), Alaska, USA. Lines represent fitted detection functions under 4 sets of analytical conditions for each park unit: diffuse priors with park unit-specific detection (dotted), informed priors with park unit-specific detection (dot-dash), diffuse priors with a common detection process among park units (dashed), and informed priors with a common detection process among park units (bold solid line). All lines are based on the mean observed group size.

detection function ($b = 1.84$; CI: 1.4–2.3) was very similar to the estimate from Schmidt et al. (2012; $b = 2.01$), and the intercept of the scale parameter corresponded to previous

Table 1. Summary of survey effort and sample sizes for Dall's sheep surveys conducted in 2010 and 2011 in Denali National Park and Preserve (DENA), the Itkillik preserve subarea of Gates of the Arctic National Park and Preserve (Itkillik), the Western Arctic National Parklands (WEAR, which includes Noatak National Preserve, Kobuk Valley National Park, and Cape Krusenstern National Monument), and Wrangell-St. Elias National Park and Preserve (WRST), Alaska, USA. Summaries are also shown for a portion of WEAR that includes all habitat north of the Noatak River (WEAR N), the western Baird Mountains subarea of WEAR (Bairds W), and the subareas consisting of northern WRST (WRST N) and southern WRST (WRST S). All surveys were conducted in 2011 except for WEAR N, which was surveyed in 2010.

Park unit	Transects completed	Total transects	No. of groups detected	Total sheep detected	Number of survey teams	Survey area (km^2)	Flight hours	Year surveyed
DENA	84	84	57	279	2	4,083	32	2011
Itkillik	39	39	48	208	1	2,542	18	2011
WEAR All	260	267	100	330	5	15,222	125	2011
WEAR N	117	124	77	206	3	7,420	54	2011
Bairds W	43	43	17	96	4	1,842	11	2011
WRST All								
WRST N	131	135	166	700	4	11,983	70	2010
WRST S	133	168	76	393	3	15,154	65	2011

Table 2. Estimated total number of Dall's sheep under 4 different sets of prior assumptions in Denali National Park and Preserve (DENA), the Iktillik preserve subarea of Gates of the Arctic National Park and Preserve (Itkillik), the Western Arctic Parklands (WEAR, which includes Noatak National Preserve, Kobuk Valley National Park, and Cape Krusenstern National Monument), a portion of WEAR that includes all habitat north of the Noatak River (WEAR N), the western Baird Mountains subarea of WEAR (Bairds W), Wrangell St. Elias National Park and Preserve (WRST), and the subareas consisting of northern WRST (WRST N) and southern WRST (WRST S), Alaska, USA. All estimates are for 2011, except WRST N, which was surveyed in 2010. Numbers in parentheses indicate 95% credible intervals and CVs represent coefficients of variation.

Park unit	Diffuse priors:units separate	Informed priors:units separate	Diffuse priors:units combined	Informed priors:units combined
DENA	7,655 (3,816–12,190) CV = 28%	2,389 (1,845–3,175) CV = 14%	2,225 (1,823–2,780) CV = 11%	2,252 (1,871–2,765) CV = 10%
Itkillik	2,808 (1,768–4,505) CV = 25%	2,276 (1,639–3,162) CV = 17%	1,653 (1,310–2,149) CV = 13%	1,669 (1,339–2,120) CV = 12%
WEAR	2,553 (2,011–3,353) CV = 14%	2,832 (2,291–3,554) CV = 11%	2,747 (2,286–3,353) CV = 10%	2,809 (2,361–3,379) CV = 9%
WEAR N	1,766 (1,352–2,374) CV = 15%	1,961 (1,546–2,524) CV = 13%	1,904 (1,543–2,382) CV = 11%	1,946 (1,593–2,397) CV = 11%
Bairds W	545 (422–736) CV = 15%	593 (455–792) CV = 15%	576 (445–752) CV = 14%	587 (457–762) CV = 14%
WRST	11,120 (9,774–12,980) CV = 7%	11,770 (10,250–13,710) CV = 7%	12,310 (10,580–14,680) CV = 8%	12,428 (10,780–14,470) CV = 8%
WRST N	7,200 (6,284–8,420) CV = 8%	7,605 (6,616–8,934) CV = 8%	7,944 (6,773–9,492) CV = 9%	8, 017 (6,915–9,417) CV = 8%
WRST S	3,962 (3,346–4,777) CV = 9%	4,204 (3,529–5,079) CV = 9%	4,412 (3,649–5,468) CV = 11%	4,456 (3,718–5,390) CV = 10%

estimates ($\beta_{int} = 0.70$; CI: 0.47–0.94) suggesting little difference in the detection process between surveys, despite much additional data. Detection probability was positively related to group size ($\ln[\beta_1] = 0.07$; CI: 0.03–0.12) and the probability of group presence was related to elevation in a curvilinear fashion ($\text{logit}[\gamma_1] = 2.33$; CI: 1.62 to 3.04; $\text{logit}[\gamma_2] = -1.97$; CI: -2.47 to -1.48). If the detection process had been substantially different in the more recent surveys,

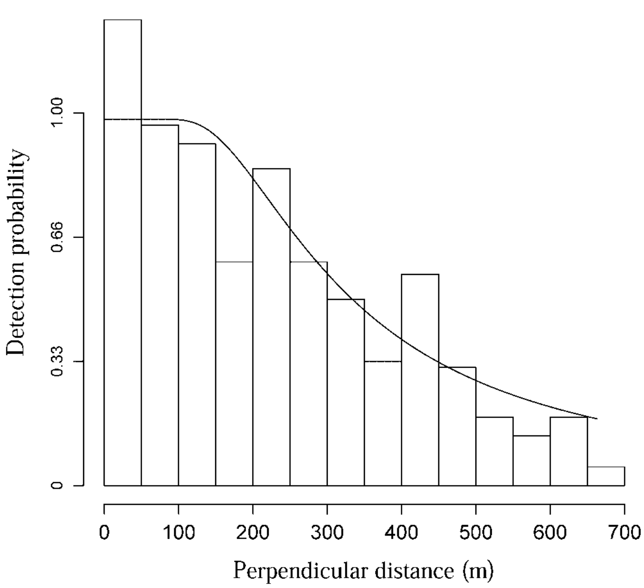

Figure 3. Histogram of perpendicular distances to all Dall's sheep groups observed in 2010–2011 in Denali National Park and Preserve, the Itkillik preserve subarea of Gates of the Arctic National Park and Preserve, Western Arctic National Parklands, and Wrangell-St. Elias National Park and Preserve, Alaska, USA combined. The solid line represents the fitted detection function based on informed priors, a common detection function among all park units, and the mean observed group size.

we would have expected the additional data to strongly influence the previous information provided through the informed priors.

Using all available information about the detection process produced estimates of abundance that were precise at the level of the individual park unit with coefficients of variation (CVs) between 8% and 12% (Table 3), well below our goal of 15%. We estimated sheep abundance to be 2,252 (1,871–2,765) in DENA, 1,669 (1,339–2,120) in the Itkillik preserve subarea, 2,809 (2,361–3,379) in WEAR, and 12,428 (10,780–14,470) in WRST (Table 3). Sheep abundance in the western Baird Mountains, a portion of WEAR of particular management concern (see Fig. 1), was less than expected at 587 (95% CI: 457–762) individuals. Combining these estimates with those from GAAR (Schmidt et al. 2012), we estimated that approximately 12,000–13,000 sheep currently occupy the available sheep habitat in the central and western Brooks Range, and approximately 26,000–27,000 Dall's sheep currently occur on all of the sampled National Park Service lands combined.

Estimates of abundance of individual composition classes and sex and age ratios were also fairly precise for most classes (except $\geq$full-curl rams) and revealed some differences in population composition among park units (Tables 3 and 4). We found that DENA had greater $\geq$full-curl ram:ewe-like ratios than both WEAR and the Itkillik preserve subarea, despite imprecise estimates for the latter 2 park units, and supported greater total ram:ewe-like ratios than WEAR. The estimated abundance of $\geq$full-curl rams was low in both the Itkillik preserve subarea and WEAR, representing around 2% of the estimated population in each area (Table 4). Apparent lamb:ewe-like ratios were 27:100, 43:100, 31:100, and 28:100 for DENA, the Itkillik preserve subarea, WEAR, and WRST, respectively. Although similar in magnitude, our estimates were greater in all 4 areas

Table 3. Estimated Dall's sheep abundance for each composition class in Denali National Park and Preserve (DENA), the Iktillik preserve subarea of Gates of the Arctic National Park and Preserve (Itkillik), the Western Arctic Parklands (WEAR, which includes Noatak National Preserve, Kobuk Valley National Park, and Cape Krusenstern National Monument), a portion of WEAR that includes all habitat north of the Noatak River (WEAR N), the western Baird Mountains subarea of WEAR (Bairds W), Wrangell St. Elias National Park and Preserve (WRST), and the subareas consisting of northern WRST (WRST N) and southern WRST (WRST S), Alaska, USA. All estimates are for 2011, except WRST N, which was surveyed in 2010. All estimates are based on the analysis using informed priors and assume a common detection function among park units. Numbers in parentheses indicate 95% credible intervals and CVs represent coefficients of variation.

Park unit	Lambs	Ewe-like	<Full-curl rams	≥Full-curl rams
DENA	350 (238–505) CV = 19%	1,128 (909–1,434) CV = 12%	582 (429–792) CV = 16%	192 (117–299) CV = 24%
Itkillik	431 (296–618) CV = 19%	903 (695–1,196) CV = 14%	296 (193–435) CV = 21%	39 (11–88) CV = 52%
WEAR	566 (420–740) CV = 14%	1,709 (1,387–2,128) CV = 11%	464 (330–639) CV = 17%	69 (29–126) CV = 37%
WEAR N	427 (314–562) CV = 15%	1,129 (873–1,460) CV = 13%	339 (233–478) CV = 19%	51 (21–95) CV = 38%
Bairds W	93 (60–141) CV = 22%	407 (313–535) CV = 14%	77 (43–126) CV = 27%	11 (4–22) CV = 44%
WRST	2,205 (1,796–2,700) CV = 10%	6,856 (5,882–8,105) CV = 8%	2,581 (2,124–3,149) CV = 10%	786 (599–1,017) CV = 14%
WRST N	1,406 (1,117–1,751) CV = 11%	4,356 (3,691–5,208) CV = 9%	1,738 (1,421–2,140) CV = 11%	516 (383–674) CV = 15%
WRST S	808 (615–1,053) CV = 14%	2,523 (2,082–3,105) CV = 10%	852 (639–1,127) CV = 15%	273 (192–375) CV = 17%

(Table 4), suggesting that observed ratios were biased because of incomplete detection. Estimates of lamb:ewe-like ratios based on the observed data suggested variation in productivity between park units, but the credible intervals of the estimates for all areas overlapped, indicating general consistency in productivity among park units (Table 4). In the western Baird Mountains area ≥full-curl ram:ewe-like and total ram:ewe-like ratios were considerably less than in DENA and WRST (Table 4). Relatively few ≥full-curl rams were detected on most surveys, resulting in abundance estimates for this class with low precision in most park units except WRST where sample sizes were greater. Abundance estimates for the remaining classes were reasonably precise with CVs ≤20% for most classes in most areas (Table 3).

DISCUSSION

Our results demonstrate that by using informed priors and borrowing detection information across surveys, reducing the recommended number of detections for Dall's sheep surveys by an additional 50–75% without a concurrent reduction in precision may be possible. Future analyses could incorporate our estimates of the shape and scale parameters of the detection function as informative priors, thereby increasing precision for survey areas where few detections are expected (e.g., small survey areas or low densities). Our approach for directly estimating population composition from distance sampling data will also provide managers with a useful tool for comparing population productivity and structure among management areas or through time while reducing logistical costs and potential bias. Combined, our approaches for abundance and composition estimation could be used to facilitate more comprehensive monitoring and effective harvest management of Dall's sheep throughout their range. In addition, the methods we describe could be easily applied to a variety of survey types and species where abundance and composition information are collected concurrently.

We found that the incorporation of hierarchical modeling techniques could be used to further reduce survey cost and effort while providing both large- and small-scale inference useful for management. Previous work established the utility of distance sampling methods for Dall's sheep population monitoring at the landscape-scale (Schmidt et al. 2012), and our current work has demonstrated that these benefits can be

Table 4. Estimated sex and age ratios and the approximate percentage of the total population representing each composition class in Denali National Park and Preserve (DENA), the Iktillik preserve subarea of Gates of the Arctic National Park and Preserve (Itkillik), the Western Arctic Parklands (WEAR, which includes Noatak National Preserve, Kobuk Valley National Park, and Cape Krusenstern National Monument), a portion of WEAR that includes all habitat north of the Noatak River (WEAR N), the western Baird Mountains subarea of WEAR (Bairds W), Wrangell St. Elias National Park and Preserve (WRST), and the subareas consisting of northern WRST (WRST N) and southern WRST (WRST S), Alaska, USA. All estimates are for 2011, except WRST N, which was surveyed in 2010. Numbers in parentheses indicate 95% credible intervals.

Park unit	≥Full-curl rams:100 ewe-like	<Full-curl rams:100 ewe-like	Total rams:100 ewe-like	Lambs:100 ewe-like	Lambs	Ewe-like	<Full-curl rams	≥Full-curl rams
DENA	17 (10–27)	52 (37–71)	69 (51–92)	31 (21–45)	16%	50%	26%	8%
Itkillik	4 (1–10)	33 (21–50)	38 (24–55)	48 (32–70)	26%	54%	18%	2%
WEAR	4 (2–8)	27 (19–38)	31 (22–43)	33 (24–45)	20%	61%	17%	2%
WEAR N	5 (2–9)	30 (20–44)	35 (23–50)	38 (27–53)	22%	58%	17%	3%
Bairds W	3 (1–5)	19 (11–31)	22 (13–34)	23 (15–34)	16%	69%	13%	2%
WRST	12 (9–15)	38 (32–45)	50 (42–57)	32 (27–39)	18%	55%	21%	6%
WRST N	12 (9–15)	40 (33–48)	52 (43–61)	32 (26–39)	18%	54%	22%	6%
WRST S	11 (8–15)	34 (26–43)	45 (36–55)	32 (25–41)	18%	57%	19%	6%

extended to more local scales by sharing detection information among surveys. The use of informative priors reduces required sample sizes and increases precision (e.g., McCarthy and Masters 2005, Link and Barker 2010, Garrard et al. 2012) because the inclusion of prior information is analogous to including all of the data in a single analysis (King et al. 2010). By using all of the available detection information, we were able to estimate abundance in DENA and the Itkillik preserve subarea with only 25–30% of the recommended sample size for a stand-alone survey (see Schmidt et al. 2012) with reasonable measures of precision (i.e., CVs = 10–12%). This suggests that our results could be used to construct priors in future analyses to provide inference for stand-alone surveys in even smaller study areas (e.g., survey areas $\leq$1,800 km^2 such as the western Baird Mountains). Over time, biologists conducting Dall's sheep surveys could build upon existing data, continually improving inference rather than treating each survey as an independent project with no information about the detection process. Sharing parameter estimates among similar projects would provide benefits to all participants through reductions in cost and disturbance, increased precision, and less risk to personnel. Using these tools, we estimated the abundance and composition of nearly 40% of the Dall's sheep population in Alaska (Heimer 1980) for the first time in almost 30 years with just 2 field seasons of effort. We expect that other sheep biologists could employ these methods at multiple scales, thereby vastly increasing the amount of robust population data available for this species, and when combined with direct estimates of composition, this could dramatically increase the scale and responsiveness of range-wide Dall's sheep management.

We also found that borrowing detection information from prior and concurrent surveys likely reduced bias in areas with small sample sizes, while increasing the precision of abundance estimates overall. Although the detection process may have differed among park units, the risk of bias caused by random variation in the patterns of detection distances within the sample in each individual park unit was probably much greater, particularly in areas with low numbers of detections. The commonalities among estimated detection functions we observed when using varying amounts of additional information to estimate the detection curve for each park unit, suggested that the assumption of a common detection process was likely met. Other available data sources also suggested that bias due to this assumption was not a major problem. For example, the estimate of approximately 1,670 sheep in the Itkillik preserve subarea corresponds with the 2009 and 2010 point estimates of 1,800–1,900 sheep for the same area (Schmidt et al. 2012) and is well within the 95% credible intervals of those previous estimates. Since the Itkillik preserve subarea contains some of the most rugged habitat in all of our survey areas, we would expect our estimate to be negatively biased if the detection process was substantially influenced by terrain. Conversely, we would have expected the estimated number of sheep in DENA (approx. 2,250) to be biased high because much of the sheep habitat in this area consisted of less rugged terrain by comparison. Although direct comparisons to past data are limited by methodological differences, we found no evidence of bias in DENA based on both historical numbers (approx. 2,500; Singer 1984*a*) and the most recent minimum count surveys (L. Phillips, National Park Service, unpublished data). These were the areas with the smallest samples most at risk for bias, so their correspondence with existing data sources suggests that differences in terrain did not dramatically influence detection. Similarities in the detection process across different habitats may be due to survey teams developing a similar search pattern over multiple surveys, diminishing the effects of terrain on detection. As future surveys are conducted in these areas, additional covariates may be included to assess any differences in the detection process related to terrain ruggedness, weather conditions, or other survey and park unit-specific factors.

A basic comparison of our abundance estimates with those from the 1980s (Singer 1984*a*, *b*) suggest that current sheep abundances are similar to historical minimum counts in most park units. The only area where abundance did not closely approximate historical estimates was in WEAR. During the 1980s, researchers counted about 1,700 sheep in this portion of the Brooks Range (Singer 1983, 1984*a*) whereas we estimated nearly 2,800 animals in the same area. Our results also suggest that the western Baird Mountains population may have declined by >30% between 2009 and 2011 (B. Shults, National Park Service, unpublished data), and the current total ram:ewe-like ratio is one of the lowest on record for this area (see Shults 2004). Interestingly, north of the Noatak River in the De Long Mountains, populations appeared to be larger than in the past, although comparable historical survey data for this area were sparse. Managers generally assumed that population dynamics were similar throughout WEAR (e.g., Westing 2008), but our results imply that these 2 subpopulations may behave independently of one another, suggesting each may require separate management and monitoring efforts.

The combination of distance sampling analytical methods with the estimation of population composition also provides several advantages for managers. Previous studies have shown strong evidence that common methods for estimating sex and age ratios are unreliable for effective management (Caughley 1974, McCullough 1994, Bonenfant et al. 2005). We presented a method for directly estimating the number of animals in each sex and age category prior to calculating sex and age ratios, avoiding the questionable assumption of a constant proportion of ewe-like sheep in the population through time while adjusting for incomplete detection. Because these ratios are based on estimates of the number of individuals in each sex and age category and include measures of precision, direct and valid comparisons across time and space are possible. For example, the apparent lamb:ewe-like ratios suggested that productivity varied among park units. However, credible intervals around the detection-corrected estimates indicated no differences were present between survey areas. The greater estimates of lamb:ewe-like ratios as compared to observed ratios suggest that ewes with lambs may occur more often in pairs or smaller groups and may be detected less frequently than other sex and age classes during surveys. Precise estimates of individual composition classes and sex and age ratios will allow managers to formally assess changes in any population component of interest, helping to identify mechanisms for variation in overall population growth rates (e.g., decreased lamb production vs. declines in ewe abundance). Also, because distance sampling surveys can cover large areas using systematic designs, estimates are more representative of the entire population of interest. Estimates based on this type of survey should be much less variable than those based on small trend count areas reliant on uncorrected indices. Accurate and representative estimates of population composition are valuable for assessing the effects of management actions or modifications to harvest regulations over time.

Although we expect that future surveys conducted in small and low density areas will benefit from the approach we have employed here, inadequate project funding can also produce sparse data. In some cases, collecting enough data to meet the recommended minimum sample size of 150–200 group detections recommended by Schmidt et al. (2012) for a stand-alone survey may be logistically or monetarily unreasonable. The approach we have described provides a rigorous, defensible method for obtaining precise, unbiased estimates of Dall's sheep abundance and composition with <50% of the detections required for an individual survey. Future Dall's sheep surveys using our protocol could directly use the parameter estimates presented here as priors for analysis, thereby incorporating all of the available prior information about the detection process. Similar projects for other species could also build upon existing data over time rather than treating annual monitoring surveys as completely independent efforts. Combined with theoretically defensible estimates of sex and age classes, our approach could facilitate more effective and responsive management of Dall's sheep populations.

MANAGEMENT IMPLICATIONS

We advocate the use of techniques combining aerial distance sampling methods with direct estimates of population composition to provide more frequent and robust assessments of Dall's sheep populations at both local and landscape scales. The use of informed priors for the parameters of the detection function, based on the results presented here and those from future surveys, can be used to reduce the number of detections required to obtain precise estimates. With this in mind, a minimum recommended sample size for future surveys of >50 group detections might be appropriate if total abundance estimation is the primary goal, with >75 group detections being preferred. If more precise estimates of the size of individual sex and age classes are desired, particularly for ≥full-curl rams, then the required number of detections would likely increase, depending on group composition. As surveys are repeated over multiple years within a survey area or for a given species, precision would be expected to increase. Using distance sampling data to directly estimate population composition should reduce both the logistical and monetary costs of Dall's sheep monitoring and should help to increase the amount of information available when setting harvest rates or taking other management actions. Our approach is not unique to Dall's sheep and could also be similarly applied to surveys for a variety of species where abundance and composition data can be collected simultaneously. Using the current estimates of Dall's sheep abundance and composition we have presented here, managers should evaluate whether the current population metrics and harvest levels meet the goals and objectives for each park unit (e.g., abundance, sex and age ratios, harvest opportunity). If objectives are not currently being met, changes to management regimes may be required.

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